

INTRASPECIFIC VARIATION IN THE BRITTLE-STAR  
*OPHIOPHOLIS ACULEATA* (LINNAEUS) IN THE  
NORTHWESTERN ATLANTIC (ECHINO-  
DERMATA; OPHIUROIDEA)<sup>1,2</sup>

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The genus *Ophiopholis* Müller and Troschel, 1842 includes several species of brittle-stars which display a considerable amount of intraspecific morphological variation. According to Clark (1911), separation of species within this genus solely on disk covering, number and arrangement of the naked aboral disk plates, length of the arm spines, shape of arm plates, and number, form and arrangement of the arm platelets, is futile. Variations in these and other characters customarily employed to distinguish ophiuroid species make it exceedingly difficult to determine reliable species characters within this genus. After examining over 5000 specimens of *Ophiopholis* from around the world, Clark (1911) concludes there are five extant species. He states *O. aculeata* is the "primary" species of the group, probably meaning it is the ancestral stock of a monophyletic group. *O. aculeata* has an Arctic—circumboreal distribution and extends southward to Japan and northern California in the North Pacific, and to Cape Hatteras and the English Channel in the North Atlantic. It normally inhabits moderate depths ranging from 0-300 meters, but a few specimens have been collected as deep as 1000 meters. Clark (1911) observed no great differences between the European and North American specimens of *O. aculeata* and none between those from the northern and southern extremes of its North American range.

A biometrical study of *O. aculeata* was undertaken to determine the morphological variability of the most ubiquitous species of this genus and to describe the differences in morphology occurring off the coasts of Maine, Newfoundland and Greenland.

METHODS AND MATERIALS

Fourteen taxonomic characters were examined statistically for three samples of *O. aculeata*. Each sample contains 200 specimens with a normal distribution of disk diameters and was collected from depths of less than 600 meters. The southern sample is from off the coast of Maine (approximate Latitude, 44°N), the intermediate sample is from off the coast of Newfoundland (approximate Latitude, 48-50°N) and the northern sample is from off the coast of southwestern Greenland (approximate Latitude, 62-67°N). Disk diameter was measured to the nearest 1.0 mm with vernier calipers. Measurements of the oral shields, arm spines and disk spines were made with an ocular micrometer to the nearest 0.03 mm. The oral shield serving as the madreporite is considerably more rounded than the other oral shields and was not used. The longest arm spine on the sixth arm

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TABLE I

*Continuous variable character comparisons between three populations of O. aculeata*

Character	Populations compared*	Observed t-value**	Coefficient of difference	Significance
Width-to-length ratio of the oral shields	1 and 2	1.20	0.05	no
	1 and 3	-3.45	0.20	yes
	2 and 3	-4.47	0.24	yes
Length of the oral disk spines	1 and 2	9.06	0.47	yes
	1 and 3	5.95	0.30	yes
	2 and 3	-1.95	0.11	no
Length of the aboral disk spines	1 and 2	-0.53	0.03	no
	1 and 3	-1.76	0.09	no
	2 and 3	-1.37	0.07	no
Number of naked aboral disk plates	1 and 2	-9.12	0.46	yes
	1 and 3	-10.18	0.55	yes
	2 and 3	-1.34	0.07	no
Number of aboral arm platelets	1 and 2	7.28	0.37	yes
	1 and 3	3.32	0.17	yes
	2 and 3	-4.26	0.21	yes

\* 1, Maine population; 2, Newfoundland population; 3, Greenland population.

\*\* In all cases there are 398 degrees of freedom and  $0.99t = 2.58$ .

segment was used for all arm spine measurements. The number of oral papillae was taken as the number occurring on five or more of the half jaws. The morphology of the oral and aboral disk spine tips was arbitrarily divided into two categories: smooth when they terminated in a rounded tip, and thorny when they terminated in a crown of thorns. The number of naked aboral disk plates does

TABLE II

*Discrete variable character comparisons between three populations of O. aculeata*

Character	Populations compared*	Observed chi-square	0.99 chi-square	Coefficient of difference	Significant
Number of oral papillae	1 and 2	2.79	6.63	0.09	no
	1 and 3	27.23	9.21	0.26	yes
	2 and 3	41.28	9.21	0.34	yes
Morphology of the oral disk spine tip	1 and 2	43.83	6.63	0.35	yes
	1 and 3	74.75	6.63	0.49	yes
	2 and 3	4.60	6.63	0.10	no
Morphology of the aboral disk spine tip	1 and 2	2.73	6.63	0.08	no
	1 and 3	0.00	6.63	0.00	no
	2 and 3	2.73	6.63	0.08	no
Number of arm spines	1 and 2	6.17	9.21	0.12	no
	1 and 3	3.61	9.21	0.08	no
	2 and 3	6.84	11.30	0.08	no
Number of naked radial shields	1 and 2	3.96	9.21	0.10	no
	1 and 3	1.24	9.21	0.02	no
	2 and 3	4.64	9.21	0.08	no
Presence of aboral arm platelet spines	1 and 2	0.25	6.63	0.03	no
	1 and 3	0.59	6.63	0.05	no
	2 and 3	0.00	6.63	0.01	no

\* 1, Maine population; 2, Newfoundland population; 3, Greenland population.

not include the naked radial shields. The radial shields were arbitrarily divided into three categories: covered, when 8-10 were covered with spines; partially covered, when 3-7 were covered with spines; and naked, when 0-2 were covered with spines. The number of aboral arm platelets was taken as the number adjacent to the aboral arm plate of the sixth arm segment. The aboral arm platelet spines were considered either present or absent.

Sample means were compared by the t-test at the 0.99 level of confidence and sample frequencies were compared by the Chi-square test at the 0.99 level of confidence. The correlation coefficient ( $r$ ) and the standard error of the regression line (S.E.) are given with all regression equations. All calculations were ob-

TABLE III

*Statistics for characters that differ significantly between populations of O. aculeata*

Character	Population	Mean	Standard deviation	Range
Width-to-length ratio of the oral shield	Maine	1.76	0.19	1.3-2.6
	Newfoundland	1.74	0.20	1.1-2.5
	Greenland	1.84	0.22	1.3-2.6
Number of oral papillae	Maine	3.32	0.53	2-5
	Newfoundland	3.42	0.59	2-6
	Greenland	3.05	0.50	2-4
Length of the oral disk spines (mm)	Maine	0.37	0.16	0.14-0.98
	Newfoundland	0.25	0.09	0.07-0.49
	Greenland	0.28	0.15	0.07-0.77
Morphology of the oral disk spine tip; 1 = smooth; 2 = thorny	Maine	1.57	0.50	1-2
	Newfoundland	1.24	0.43	1-2
	Greenland	1.15	0.36	1-2
Number of naked aboral disk plates	Maine	31.58	12.63	0-84
	Newfoundland	44.77	16.08	12-105
	Greenland	47.01	17.30	10-133
Number of aboral arm platelets	Maine	16.31	2.57	9-26
	Newfoundland	14.70	1.80	10-22
	Greenland	15.53	2.11	12-23

tained by the use of a Fortran PDIFF program on the University of Maine IBM-360 computer.

## RESULTS

### *The oral surface of the disk*

Mean length-to-width ratios of the oral shields (Tables I and III) are essentially the same in the Maine and Newfoundland samples but are significantly greater in the Greenland sample. This ratio ranges from 1.1-2.6 for the species, or from nearly circular to oval.

The mean number of oral papillae (Tables II and III) is essentially the same in the Maine and Newfoundland samples but is significantly less in the Greenland sample. The number of oral papillae increases with an increase in mean disk diameter (Table IV).

TABLE IV

*Statistics for discretely variable characters of O. aculeata that change with size\**

Character	Class	N	Mean of disk diam. (mm)**	Standard deviation (mm)	Range (mm)
Number of arm spines	(4)	11	2.6	0.81	2-4
	(5)	203	7.4	2.43	2-14
	(6)	329	11.2	2.54	6-19
	(7)	57	13.8	2.35	10-19
Number of oral papillae	(2)	24	5.5	2.78	2-11
	(3)	403	9.7	3.20	2-19
	(4)	165	11.3	3.13	5-19
	(5)	6	13.7	2.34	10-17
	(6)	2	10.0	3.38	12-14
Aboral arm platelet spines	(present)	23	4.1	1.96	2-8
	(absent)	577	10.2	3.20	2-19

\* All populations were considered together.

\*\* The mean of the disk diameters was calculated for each class.

The mean length of the longest oral disk spines (Tables I and III) is essentially the same in the Newfoundland and Greenland samples but is significantly longer in the Maine sample. An increase in length of oral disk spines is correlated with an increase in disk diameter, but the correlation coefficients are low, varying from 0.64-0.69 for the three samples.

The morphology of the oral disk spine tips (Tables II and III) differs significantly between Maine and Newfoundland but is essentially the same in New-

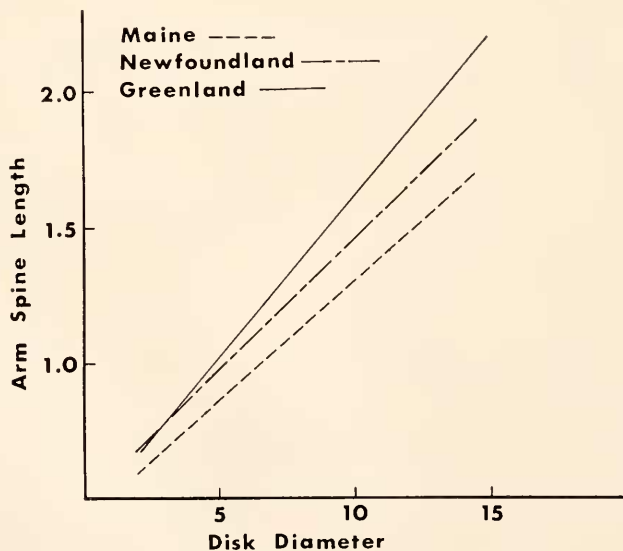


FIGURE 1. Linear regression lines for arm spine length as a function of disk diameter in the three populations of *O. aculeata*. All measurements are in millimeters.

foundland and Greenland. The frequency of specimens with thorny spine tips decreases clinally from 57–15 per cent, from Maine to Greenland.

#### *The aboral surface of the disk*

The mean length of the longest aboral disk spines (Table I) does not significantly differ between the three samples. An increase in spine length is correlated with an increase in disk diameter, but the correlation coefficients of the linear regression lines are low, ranging from 0.63–0.76.

The morphology of the aboral disk spine tip (Table II) does not significantly differ between the three samples. The frequency of specimens with thorny aboral spine tips ranges from 4–8 per cent for the three samples.

The number of naked radial shields is not significantly different in the three samples (Table II). Specimens with covered radial shields comprise 62.5 per cent of the combined samples, those with naked shields comprise 29.0 per cent and those with partially covered radial shields comprise 8.5 per cent of the combined samples.

The mean number of naked aboral disk plates (Tables I and III) increases along a cline from 32 in the Maine sample to 47 in the Greenland sample. This number is not correlated with disk diameter.

#### *The arms*

The mean number of aboral arm platelets (Tables I and III) differs significantly between the three samples, but does not vary clinally. The Maine sample has the largest mean of 16.3 and the Newfoundland sample has the smallest mean of 14.7. The Greenland sample is intermediate with a mean of 15.5 platelets.

There is no significant difference between the samples for the presence of aboral arm platelet spines (Table II). Platelet spines are present only on small specimens (Table IV) with a disk diameter of 8 mm or less. The spines do not occur on all small specimens since individuals as small as 2 mm were without platelet spines.

The frequencies for the number of arm spines (Table II) are essentially the same in all the samples. The number of arm spines increases from 4–7 with an increase in mean disk diameter from 2.6–13.8 mm (Table IV).

The length of the arm spines increases linearly with an increase in disk diameter (Fig. 1). The arm spines increase clinally in relative length from the Maine to the Greenland sample. The slope for the Greenland sample is significantly greater than the slopes of the more southern samples. Even though the slopes for the Maine and Newfoundland samples are not significantly different, the y-intercept is significantly greater in the latter, resulting in proportionately shorter arm spines in the Maine sample. The regression equations are:

Maine	$y = 0.90.r + 0.44, r = 0.86, \text{S.E.} = \pm 0.13 \text{ mm}$
Newfoundland	$y = 0.96.r + 0.50, r = 0.86, \text{S.E.} = \pm 0.13 \text{ mm}$
Greenland	$y = 1.20.r + 0.41, r = 0.84, \text{S.E.} = \pm 0.19 \text{ mm}$
	$y = \text{arm spine length (mm)}$
	$r = \text{disk diameter (mm)}$

The width of the arm spines increases linearly with an increase in disk diameter. The slopes and  $y$ -intercepts of the regression line do not differ significantly between the three samples. The regression equation for the combined sample is:

$$y = 0.81x - 0.01, r = 0.93, \text{S.E.} = \pm 0.07 \text{ mm}$$

$y$  = arm spine width (mm)  
 $x$  = disk diameter (mm)

The width of the arm spines increases linearly with an increase in arm spine length (Fig. 2). As shown above, arm spine length increases clinally with increase in latitude, but the width remains constant. This results in the arm spines being

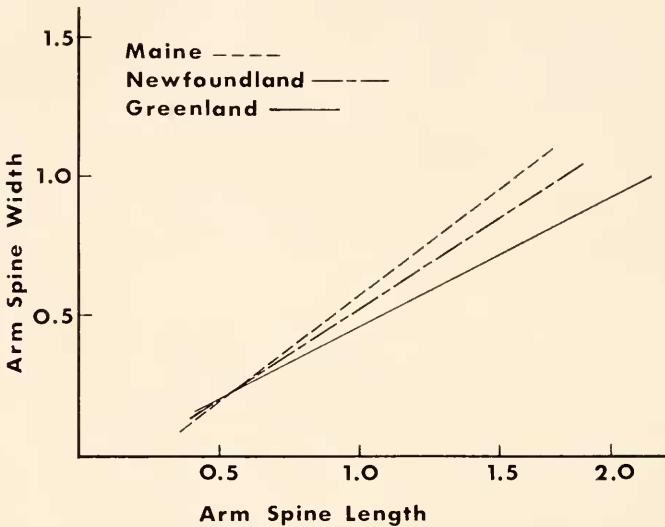


FIGURE 2. Linear regression lines for arm spine width as a function of arm spine length for the three populations of *O. aculeata*. All measurements are in millimeters.

more acute in the more northern latitudes. Slopes for the linear regression lines differ significantly between the three samples. The regression equations are:

Maine	$y = 0.72x - 0.21, r = 0.89, \text{S.E.} = \pm 0.11 \text{ mm}$
Newfoundland	$y = 0.63x - 0.16, r = 0.80, \text{S.E.} = \pm 0.21 \text{ mm}$
Greenland	$y = 0.49x - 0.09, r = 0.83, \text{S.E.} = \pm 0.19 \text{ mm}$
	$y$ = arm spine width (mm)
	$x$ = arm spine length (mm)

#### DISCUSSION

Characters that change clinally include (1) number of naked aboral disk plates, (2) length of the arm spines, and (3) length-to-width ratio of the arm spines.

Characters that are essentially the same in Maine and Newfoundland, but are distinctly different in Greenland include (1) length-to-width ratio of the oral shields, and (2) number of oral papillae.



Characters that are essentially the same in Newfoundland and Greenland, but are distinctly different in Maine include (1) length of the oral disk spines, and (2) morphology of the oral disk spine tip.

A character that does not change clinally but is distinctly different in all populations is the number of aboral arm platelets.

Characters that are essentially the same in all populations include (1) morphology of the aboral disk spine tip, (2) number of naked radial shields, (3) presence of aboral arm platelet spines, (4) length of the aboral disk spines, (5) width of the arm spines, and (6) number of arm spines.

None of the above characters are sufficiently different between samples that their coefficient of difference approaches the 1.28 value suggested by Mayr (1969) to be a basis for subspecific distinction. The magnitude of the differences is large enough to indicate the samples came from three phenotypically distinct populations. The uniformity of some characters in all the populations may indicate the expression of these characters is not significantly altered by environmental factors, such as temperature or salinity. Those characters that vary clinally between populations are probably under the influence of some environmental parameter.

Two meristic ranges given for *O. aculeata* by previous workers, are too small. Mortensen (1927) and Dyakonov (1954) state there are 3 (rarely 2) oral papillae in *O. aculeata*. The present study shows there are 2-6 oral papillae with most specimens having 3-4. The number of arm spines ranges from 6-7, according to Mortensen (1927), and 5-7 according to Dyakonov (1954). The present study shows a range of 4-8. None of the specimens used in this study had more than 7 arm spines; however, some very large specimens, 22 mm in disk diameter or greater, had 8 arm spines on the sixth arm segment. Because the number of oral papillae and number of arm spines is size dependent, expansions in these ranges are expected when examining extremely small or large specimens.

Grieg (1893), cited in Mortensen (1933), states that Greenland specimens of *O. aculeata* are more spiny on the disk than ones from the Norwegian coast. According to Mortensen (1933), a large percentage of the Greenland specimens collected during the Danish Ingolf-Expedition had long spines on the disk. These spines were most prominent along the borders of the radial shields. He noted that they were particularly evident on specimens from the more northern localities with negative bottom temperatures. Clark (1911) notes that Alaskan specimens of *O. aculeata* have a more spinous disk than ones from Maine. This study indicates the oral disk spines of the Maine sample are significantly longer than those of the Newfoundland or Greenland samples and the aboral spine length is essentially the same in all three samples. A few specimens in the United States National Museum, Washington, D. C. and the Museum of Comparative Zoology, Harvard University, collected in the high Arctic have very long aboral disk spines, particularly around the radial shields. If the aboral disk spines are significantly longer in the specimens from the high Arctic, then the increase in length must occur somewhere north of the northernmost sampling area used in this study (approximate Latitude, 67°N).

Dyakonov (1954) described *O. pilosa* from the Sea of Okhotsk. This species is supposed to differ from *O. aculeata* in the following ways: 1) Short spinelets occur along the edge of the disk and terminate in a sharp thorn or crown of thorns;

2) The aboral arm platelets are numerous, small, rounded, and usually possess a spine; 3) The radial shields are naked. All these characters fall well within the range of variation displayed by *O. aculeata*. This makes the validity of *O. pilosa* questionable. A reevaluation of *O. pilosa* will probably indicate it is a junior synonym of *O. aculeata*.

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#### SUMMARY

1. Fourteen taxonomic characters were analyzed separately for Maine, Newfoundland and Greenland populations of *O. aculeata*.

2. The number of naked aboral disk plates, length of the arm spines and length-to-width ratio of the arm spines are characters that vary clinally.

3. The length-to-width ratio of the oral shields and the number of oral papillae are essentially the same in the Maine and Newfoundland populations but are significantly different in the Greenland population.

4. The length of the oral disk spines and morphology of the oral disk spine tip are essentially the same in the Newfoundland and Greenland populations but are significantly different in the Maine population.

5. The number of aboral arm platelets does not change clinally but is distinctly different in all populations.

6. The morphology of the oral disk spine tip, number of naked radial shields, presence of aboral arm platelet spines, length of the aboral disk spines, width of the arm spines and number of arm spines are characters essentially the same in all populations.

7. There are 2-6 oral papillae and 4-8 proximal arm spines present on *O. aculeata*.

8. The diagnostic characters of *O. pilosa* Dyakonov, 1954, fall within the range of variation displayed by *O. aculeata*.

#### LITERATURE CITED

- CLARK, H. L., 1911. North Pacific ophiurans in the collection of the United States National Museum. *U. S. Nat. Mus. Bull.*, 75: 1-302.
- DYAKONOV, A. M., 1954. *Ophiuroids of the USSR Seas*. Izdatel'stvo Akademii Nauk SSSR Moskva-Leningrad, 131 p. [Translated from Russian, 1967, by the Israel Program for Scientific Translations, Jerusalem, TT 67-51490.]
- GRIEG, J. A., 1893. Ophiuroidea. *Norske Nordhav's Expedition 1876-1878, Zool. (Christiania)*, 23: 1-41.
- MAYR, E., 1969. *Principals of Systematic Zoology*. McGraw-Hill Book Company, New York, 428 pp.
- MORTENSEN, T., 1927. *Handbook of the Echinoderms of the British Isles*. Oxford University Press, New York, 421 pp.
- MORTENSEN, T., 1933. Ophiuroidea. *Danish Ingolf-Expedition*, 4(8): 1-121.